XXXV. — *Studies on the Charadriiformes.* — II. *On the Osteology of the Chatham Island Snipe* (Cœnocorypha pusilla *Buller*). By Percy R. Lowe, M.B., M.B.O.U.

(Plate VIII.; Text-figures 12–14.)

The ultimate objects which ornithologists have in view are, I take it, first, to acquire as complete a knowledge of present existing birds as is possible; secondly, to co-relate this knowledge with what we know of the birds of past geological ages; and, finally, out of the sum of knowledge thus obtained, to construct an ideal genealogical tree, which shall demonstrate in as vivid a way as possible the phylogenetic relationships and history of the whole class under consideration. In attempting to do this, ornithologists are, perhaps, handicapped to a greater extent than any other class of zoologists, chiefly owing to the gaps in the geological record. Imperfect as this record is in every branch of the animal kingdom, it is, I think, an admitted fact that in the class Aves the record is more imperfect than in any other. As a compensating factor to set against this undoubted handicap we have, however, an asset which I am inclined to think is sometimes overlooked. I refer, of course, to the extraordinary *persistency* of bird-types. As a result of this persistency, we not only find that certain birds of to-day present the most surprising likeness to the birds of, let us say, a geological age as far back as the Pliocene or Miocene, but that in the present age we meet with many types which are for all practical purposes "living fossils."

Of these "living fossils" we must, in lieu of fossils proper, make the most we can. So far as one has been able to gather from an examination of a complete skeleton in the British Museum, the Chatham Island Snipe might be said with very little exaggeration to be one of these "living fossils,"—there is little doubt, at any rate, that it is an ancient and generalised Snipe, which from the point of view of the phylogeny of the Scolopacinæ is of great interest.

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SKULLS OF SCOLOPACINE AND ALLIED FORMS.

1. Rhynchea bengalensis. 2. Homoptilura gigantea. 3. Erolia alpina.
4. Coenocorypha pusilla. 5. Lymnocryptes gallinula. 6. Gallinago gallinago.
7. Scolopax rusticola. 7a. S. rusticola; tarso-metatarsus, posterior view. $\frac{2}{3}$
4a. C. pusilla; tarso-metatarsus, posterior view. $\frac{2}{1}$

The Chatham Island Snipe is resident in the extreme south, and, like many other types of Waders found in southern or ultra-southern latitudes, its characters present us with a picture in interesting contrast with those proper to more northern types.

Taking, for instance, Waders whose present distribution is confined roughly to regions south of the equator, and excluding certain migratory types or types with a world-wide range, we find in this southern half of the globe many Waders whose characters seem to present a general picture which can only be taken to correspond to a geological era anterior to the present one. The impression which we get, and the conclusion which it seems difficult to escape, appears to be, that this peculiar southern Wader-fauna has been forced southwards towards the southern extremities of the great land-masses of the world by adverse conditions, either climatic, physical, or faunal, which obtained in the north; and that it represents to a great extent the relics of a fauna which had at one time a more extensive northerly distribution or origin.

Examples among the southern Waders of such an old-time fauna which occur to one at once are the following:—The Jacanas (Jacanidæ), the Painted Snipe (Rhynchæidæ), the Stone-Curlews (Œdicnemidæ), the Seed-Snipes (Attagidæ), and the Sheathbills (Chionidæ), together with such peculiar types as the Slender-billed Plover (*Oreophilus*), the Chilian Sandpiper (*Phegornis*), the Magellanic Plover (*Pluvianellus*), the New Zealand Plover (*Thinornis*), the Black-fronted Dotterel of Australia (*Elseyornis*), and, finally, that group in which the Chatham Island Snipe may itself be included, viz., Seebohm's "semi-Woodcocks." These "semi-Woodcocks" of Seebohm comprise, in addition to the genus *Cœnocorypha*, such highly interesting South American forms as *Gallinago stricklandi* Gray of the Chilian Andes, *G. jamesoni* Bonaparte of the Peruvian Andes, *G. imperialis* Sclater of Colombia, *Homoptilura undulata* (Bodd.) of the mountains of Guiana, and *H. undulata gigantea* (Natterer) of Brazil. These last are found in very elevated forested mountains, sometimes

as high as 7000 feet, and, judging from a skull of the last-mentioned form, to be noticed hereafter, they are more Rusticoline than Gallinagine. Seebohm coined his term "semi-Woodcock" after examination of skins only. He found, however, that the colour-pattern characteristic of the South American forms was much more Gallinagine than Rusticoline, although it is interesting to note that without the aid of osteology he practically summed up the correct nature of these birds, viz., that they were generalised Snipe-like forms—neither true Woodcocks nor true Snipe. Unfortunately, with the exception of the skull of *Homoptilura*, there is no available material in the British Museum wherewith to examine the osteological secrets of this extremely interesting and generalised group, which might throw so much light on the past history of the Scolopacine subfamily. Specimens in the flesh of all such forms are badly wanted.

The more one studies these and the other southern forms mentioned above, the more impressed one becomes with the fact that in them we have what it is hardly an exaggeration to call a series of "living fossils." They are persistent relics of diverging branches which shot from the old ancestral trunk—branches which, although they seem to have arrived at a blind alley of evolution, reflect in some of their peculiarities a greater or lesser number of the features which must have characterised the original ancestral stock. They would appear to represent disconnected stages in the gradual (or sudden) evolutionary unfoldings of the Limicoline germinal plasm, and the question is—Do they furnish us with any hints which will put us on the right track in attempting to retrace the evolutionary path pursued by their more modern congeners? There are points in the osteological features presented by *Cœnocorypha pusilla* of the Chatham Islands which might be interpreted in this sense, and, since the skeletal features of this form have never, so far as I am aware, been previously described, I propose to consider them in this paper.

There are, however, one or two preliminary points to

which I should like to refer before commencing this account. I have said that there is good reason to regard the Chatham Island Snipe as an ancient and generalised form—apparently the most generalised Snipe-like form of which we have any evidence—and that its present habitat is ultra-southern. Have we any right to assume, as is invariably done in other like cases, that the present-day habitat of this the most generalised Scolopacine form represents the centre of dispersal (or part of the original focus of dispersal) of the Scolopacine race? In a recent and most interesting paper on "Climate and Evolution," Dr. W. D. Matthew (Annals N.Y. Acad. Sci. vol. xxiv. 1915, pp. 171–318) has stated as his opinion that such an assumption as regards generalised members of other groups is "wholly illogical." "Whatever agencies," he says (p. 180), "may be assigned as the cause of evolution of a race, it should be at first most progressive at its point of original dispersal, and it will continue this progress at that point in response to whatever stimulus originally caused it and spread out in successive waves of migration. . . . . At any one time, therefore, the most advanced stages should be nearest the centre of dispersal, the most conservative stages farthest from it. In the same way, in considering the evidence from extinct species as to the centre of dispersal of a race, it has frequently been assumed that the region where the most primitive member of a race has been found should be regarded as the source of the race, although in some instances more advanced species of the same race were living at the same time in other regions. The discovery of very primitive Sirenians in Egypt, while at the same time much more advanced Sirenians were living in Europe, has been regarded as evidence that Africa was the centre of dispersal of this order. *It is to my mind good evidence that it was not* (italics mine). . . . . it is much more correct to say that the modern African fauna is of Tertiary aspect, and is in large part the late Tertiary fauna of the northern world, driven southward by climatic change and the competition of higher types."

With the evidence which we shall shortly give of the generalised nature of the species comprising the genus *Cœnocorypha* of the ultra-south, and of those peculiar South American forms comprising the group of gigantic Scolopacine species which are neither wholly Rusticoline nor wholly Gallinagine, and which Seebohm called semi-Woodcocks, the views put forward by Matthew are of great interest. If we agree, for instance, with his conclusions and for the present ignore all consideration of the ancient Antarctica, it is evident that the original centre of dispersal and evolution of the Snipes was in the north.

But it might conduce to the interest of this aspect of the past history of the genus *Cœnocorypha* if we add the few following remarks which are ancillary to the subject.

The Chatham Islands comprise a small isolated group some five hundred miles to the east of New Zealand. At the present day, the only island of the group inhabited by *C. pusilla* is a small outlier named Mangare ; but we may feel certain that this present-day restriction is simply due to extermination of the species on the other islands subsequent to the arrival of man and of carnivorous animals * introduced by him †.

Allied forms of *C. pusilla* are found on the Auckland Islands (*C. aucklandica* Gray) and on Snares Island (*C. heugeli* Tristram). I have not had the opportunity of examining the osteological features of these two species, but we may, I think, take it for granted that in all essential points they are similar to those of *C. pusilla*. There is no reliable record of any species of *Cœnocorypha* ever having been taken in New Zealand, nor have any fossil relics been obtained there. Nevertheless, it appears not improbable that some form of this genus must have originally inhabited New Zealand, but that since the advent of man all traces of it have disappeared. In connection with this curious absence it is interesting to reflect that no other

* *Cœnocorypha* is on the way to become flightless.

† Since this was written I have found sub-fossil forms of *C. pusilla* from Wharekauri (Chathams) in the collections of Lord Rothschild and Dr. H. O. Forbes.

resident species of Snipe (*Gallinago*) is known from either New Zealand or Australia—or, for that matter, from India (excluding high mountainous regions of the north) or the Malay Archipelago.

This allusion to the absence of *Cœnocorypha* from New Zealand introduces us, however, to a very brief notice of the geological and other evidence bearing on the question whether the Chathams (and the other islands mentioned) were or were not connected in Tertiary times with Australia or New Zealand, for it is obvious that this question is one which bears on the past history of *Cœnocorypha*, and through that genus on the whole history of the Scolopacine subfamily.

Hutton (Index Faunæ Novæ Zeland.), after stating that the Chathams consist of fossiliferous limestones (and clay slates) of early Miocene age resting on a low platform of ancient schistose rocks, mentions the presence of fresh-water species of *Galaxias* * which are similar to those of New Zealand and "which do not appear to go down to the sea." On Pitt Island (one of the Chathams) there is a lizard closely related to *Lygosoma moko* † of New Zealand. The Chathams and Aucklands have also small forest-birds, as well as slugs and beetles, "none of which could cross over a sea-barrier." Hutton concludes, therefore, that the Chathams and the other neighbouring islands were once connected with New Zealand, and derived the main part of their fauna overland. He thinks that the number of endemic species and even genera among the land-animals of all these islands proves that they have been long separated, and altogether precludes the idea of a comparatively recent Antarctic continent connected with New Zealand. They also preclude the idea of a very cold climate having existed in the Southern Hemisphere since the islands were separated from New Zealand—that is, since the Pliocene.

Andrews ('Novitates Zoologicæ,' vol. iii. 1896, pp. 73, 260) believes that there is nothing in the present fauna of the

* It is now known that the Galaxiidæ breed in the sea.

† *Lygosoma* is a genus of wide distribution in the Pacific and elsewhere and is obviously capable of transporting itself over sea.

Chathams to show that since their last emergence (Pliocene) they have been connected with any land-area whatever. "On the contrary," he says, "it seems clear that since that period they have never been united even with New Zealand, for not a trace of any of the Dinornithidæ, *Apteryx*, *Cnemiornis*, *Aptornis*, or any of the flightless birds characteristic of those islands, have been found on them. Moreover, as Dr. H. O. Forbes himself has pointed out, no fragments of the skeleton of *Diaphorapteryx* are recorded from the ancient land-mass of New Zealand." It seems clear, therefore, that the Chathams and Aucklands have been separated for a very considerable period from New Zealand, but that, nevertheless, the species of the genus *Cœnocorypha* have been derived from a stock which originally hailed from that land-mass. But it is also obvious that this stock did not arise *de novo* in the ancient antipodes, and that it must have been derived from a still more ancient and more northerly living stock—in other words, these ultra-southern Snipe came originally "radiating from the north."

On the other hand, there are those who would hold that the great likeness which Strickland's Snipe (*Gallinago stricklandi*) of the Straits of Magellan and Chile (as well as the other generalised antipodean Snipe previously mentioned) bears to these Chatham Island Snipe points to the supposition that they all came "radiating from the south." Behind the striking similarity of form which exists in the resident Snipe of these isolated and widely separated southern extremities of the Old and New World, looms, they would hold, the ancient Antarctic continent.

Dr. H. O. Forbes, in an interesting paper read before the Royal Geographical Society in 1893 on the relation of the Chatham Islands to a former southern continent, held, for instance, much the same views.

Except in its greater size and more Snipe-like colouring, Strickland's Snipe in all superficial (and, for all we know, in all deeper-lying) characters *is* astonishingly similar to the Chatham and Auckland Snipes. Its tarsus is Rusticoline (scutellate in front, reticulate behind), its legs and toes are

Rusticoline (short and thick with a pad under claw of hind toe), its bill is Rusticoline, its tail and wings are Gallinagine. But that these forms are relics of an ancient and cosmopolitan common ancestor hailing from the north, or that they are instances of parallelism, seems easier to believe than that they owe any thing of their similarity to an ancient Antarctic connecting-bridge. Moreover, in a review of the fishes obtained in the 'Terra Nova' Expedition, together with a critical examination of the evidence derived from the supposed relationships of *Thylacinus* of Tasmania and the Sparassodonts of the Patagonian Miocene strata, Mr. Tate Regan has lately dealt the hypothesis of an ancient Antarctic bridge connecting the Australian continent with South America in Tertiary times a severe blow (*cf.* Brit. Mus. Rep. 'Terra Nova' Exp., Fishes, 1914).

On the largest island of the Chatham group (Wharekauri —thirty-six miles by twenty-seven) fossil remains of the genus *Cœnocorypha* were discovered by H. O. Forbes in Pleistocene deposits, and received from him the specific name of *Gallinago chathamica*. In his original description Forbes simply states that this fossil form is "a very much larger species than *G. pusilla*. The bill is three inches in length" (*cf.* 'Ibis,' 1893, p. 545).

While studying the skeletal features of *C. pusilla*, Miss D. M. A. Bate kindly called my attention to the fact that there was a large collection of fossil bird-remains from Chatham Island in the British Museum collection, and among them we found specimens of the skulls of this fossil Snipe, *C. chathamica*. Except that their measurements are larger, the skulls of all the specimens of *C. chathamica* which I have examined agree in every particular with the skull of *C. pusilla*. It is interesting, however, to note that the præmaxillæ of these fossil specimens vary greatly in length, even if we allow for differences in the measurements due to sex. Thus in *C. chathamica* the following represent measurements from the tip of the præmaxillæ to a line forming the proximal ends of the outer processes of the nasals:—77 mm. and 75 mm. (in the two types contained in the Brit. Mus.

Coll.), 76 mm., 71 mm., 71 mm., 69 mm., 68 mm., and 63 mm. in six examples contained in Lord Rothschild's collection * ; whereas the same measurements in the skull of the present existing *C. pusilla* works out at 54 mm.

Practically similar measurements to this last (54 mm. and 54·5 mm.) were noted in the skulls of two examples of *C. pusilla* found subfossil in the same sand-bank as contained the above subfossil remains of *C. chathamica*. Variation, as is well known, is very prone to run amok in the case of flightless birds on isolated islands where enemies are few, so that the varying measurements in *C. chathamica* might be taken to indicate toleration on the part of natural selection. On the other hand, it is just possible that they might be taken as indicative of a gradual grading of the one form into the other, so that in *C. pusilla* of the present day we have a *direct* lineal descendant of *C. chathamica*—or, in a word, that the two forms represent in reality one species, exhibiting a diminishing and continuous series of gradations. Such, however, does not necessarily follow, and it may be pointed out that in the Chatham group two distinct species of *Cabalus* are known to have existed, not to mention other forms.

The point seems to me to be worth consideration in connection with the question whether the normal process of evolution is a gradual or a discontinuous process.

At the present day *C. pusilla* has so far lost the power of flight that it can be easily knocked down by a stick, although when it first rises it is said to exhibit a feeble imitation of the twists and turns of its more northern congeners before it sinks to the ground some twenty yards from the spot where it rose. Other points in connection with the peculiarities of this interesting "Snipe" are as follows :—its eggs are not Gallinagine in either shape or colouring, the shape being a compromise between the typical Gallinagine and the typical Rusticoline form and the colouring being reminiscent

* For permission to examine these fossil remains from the Chatham Islands now preserved in the Tring Museum I am greatly indebted to Lord Rothschild.

of the Rail's eggs. The appearance of the nestling young is also aberrant in virtue of the absence of all markings whatever, the downy plumage above being of a uniform umber-brown coloration. The nestling young of *Chionis minor* of the Antarctic islands also exhibits this same uniform brown coloration, but it is to be noted that both birds seem to nest in as protected and as dark situations as they can find.

So far as one can gather from accounts of its habits, the Chatham Island Snipe seems to be more than usually nocturnal, for it is said to hide in the daytime in hollow trunks or tree-stumps, or in any scrap of cover protected from the light.

Description of the skull of Cœnocorypha *as seen from above.*

(*a*) If the skull of *C. pusilla* is examined from above and compared with similar aspects of the skulls of the Woodcock, Common Snipe, Jack-Snipe, and Dunlin (*cf.* Pl. VIII. figs. 3–7), we are at once struck with the fact that, as regards its general configuration and outline, the skull of the Chatham Island Snipe approaches the skull of the Dunlin much nearer than is the case with regard to either the Woodcock, the Common Snipe, or the Jack-Snipe. In *C. pusilla*, for instance, we miss the peculiar oval outline of the hinder part of the skull (that part caudad of the pre-maxillæ, nasals, etc.) so characteristic of the true Scolopacine type. In figs. 5–7 we see this oval or ovate configuration of the Scolopacine skull well depicted. In them, too, one notes that the outer margins of the lacrymals and the superior and inferior orbital rims merge one into the other in one continuous and smoothly curved outline. If this contrast between the two types of skull depicted in figures 3–7 is appreciated, it will be still more apparent in the case of the skull of the Painted Snipe (*Rhynchæa*) seen in fig. 1.

(*b*) The backward position of the orbital cavity, so characteristic of the true Snipe (Scolopacinæ), more especially of the Woodcocks, is also conspicuous by its absence

in the Chatham Island Snipe, in which we have an approach to the Eroliine condition (*cf.* fig. 3). The same may be said in regard to the Painted Snipe (fig. 1).

(*c*) In the Chatham Island Snipe the outer edges of the orbital processes of the lacrymals make an angle with the orbital rims, instead of gradually merging with them in a continuous and uninterrupted curve, so characteristic of the typical Scolopacine form. A reference to the figures already indicated should make this point clear. In figures 5–7, for instance, the lacrymals are observed to be very typical ear-shaped processes gradually curving forwards, inwards, and downwards to a pointed extremity, while in fig. 4 the lacrymals of *C. pusilla* are projected laterally in a more abrupt and conspicuous way. Anteriorly (but this cannot be seen in the figure) the lacrymals of *C. pusilla* are noted to be Scolopacine in general shape, but they are aberrant in their narrow elongate form and in their more intimate contact with the outer nasal processes.

In respect of the lacrymals of the Painted Snipe these (in an actual specimen) are seen to come nearer the Vanelline form and shape than to any other form with which I am acquainted. In the true Scolopacine type, as we shall later see, the entire posterior surface of the descending lacrymals fuses with the antorbital plate, this part of the lacrymal almost losing its identity in the process. In *Rhynchæa* the descending lacrymal is free and independent throughout most of its extent. Its distal extremity merely fuses with the extero-inferior angle of the antorbital plate, and the whole lacrymal has, as I have said, very nearly the same form and shape as in *Vanellus*. Attention is also directed to the sharp outwardly projecting process formed by the orbital portion of the lacrymal in *Rhynchæa* and its un-Snipe-like appearance.

(*d*) If an imaginary line be drawn at right angles to the longitudinal axis of the skulls of the Chatham Island Snipe, Dunlin, and Painted Snipe from the hinder margins of the orbit of either side, we are at once struck with the much

greater relative dimensions of the brain-pan caudad of this line, both in coronal and sagittal section, than obtains in the case of the Woodcock, Common Snipe, and Jack-Snipe, the comparative disproportion in dimensions being most noticeable in the case of the Woodcock and less so in the Jack-Snipe (*cf.* figures).

The same Snipe-like contrast is noted in the case of figure 2, which depicts the skull of *Homoptilura*.

(*e*) Another comparative point of distinction which may be observed by a reference to these figures is the conspicuous visibility of the quadrates in the case of the skulls of *C. pusilla*, *Erolia*, and *Rhynchæa*, as observed from this dorsal aspect, and the degree in which they project laterad of the lacrymals. In comparison with what obtains in the case of figs. 5–7 detailed description seems unnecessary; but attention is called to the conspicuousness of the mandibular process in *Homoptilura* in comparison with that noted in *Scolopax*. The relative forward or backward position of the quadrates in all seven forms shown should be noted.

(*f*) It is, however, when we come to compare the interorbital region of all these forms that we are perhaps most struck with the anomalous appearance of the skull of the Chatham Island Snipe when viewed from this dorsal aspect. In *Scolopax*, *Gallinago*, *Lymnocryptes*, and *Homoptilura* this interorbital region is deeply grooved or furrowed, while its margins are raised, arched, moulded, corniced, and somewhat falcate. In *Cœnocorypha*, on the other hand, this same region appears narrow, smooth, and flat (the shallow furrow being only obvious on minute examination), its borders are more nearly parallel and its rims are neither raised, moulded, nor arched. A curious fact to be noted in the actual specimen is that the grooves for the supraorbital glands are situated on the very outer *edge* of the orbital rim—that is to say, that they look *directly outwards*. They can only be seen from a lateral aspect of the skull. In the genera above mentioned there are no supra-orbital glandular grooves. The general similarity of the interorbital region in *Cœnocorypha* to those

of *Erolia* and *Rhynchæa* is to be noted. The interorbital region of *Cœnocorypha* is, however, suggestively Eroliine, that of *Rhynchæa* Tringine.

Narrow as the interorbital region is seen to be in the present-day skull of *C. pusilla* (fig. 4), it is still narrower in two subfossil examples dug up with other fossil bird-remains on the Chathams. The comparative measurements, for example, are as follows:—In *C. pusilla* the width was 4 mm.; whereas in the two subfossil forms of *C. pusilla* it was 3·5 mm. and 3·0 mm. respectively. The last-mentioned measurement represents roughly the width of the interorbital region in *Erolia alpina* (fig. 3).

Transferring our scrutiny to the anterior portion of the skull, it is obvious that in the Chatham Island Snipe the premaxillæ and associated processes are very distinctly more Rusticoline in form and structure than Gallinagine. The premaxillæ and premaxillary processes of a typical Woodcock and a typical Snipe are easily to be distinguished. Want of space forbids a detailed description of the differences, but in Pl. VIII. figs. 4–7 the four premaxillæ easily group themselves into two categories—Rusticoline and Gallinagine. We would draw attention, however, to the spatulate and flattened condition of the foveated ends of the premaxillæ in the Gallinagine type, to their thin flexible nature, to the flattening out of the culmen-ridge at the foveated extremity, to the way in which the more rounded and slender maxillary processes of the premaxillæ underlie the culmen-ridge in *Gallinago* (not, I think, due to elastic tension in the dried skeleton), and to the different detailed character and extent of the sculpturing, *in relief*, of the honeycomb-like circular or oval cells so characteristic of the foveated end of the bills in the Scolopacinæ and Eroliinæ (*cf.* also 'Ibis,' 1915, p. 612).

The premaxillæ of the Rusticoline type present exactly opposite conditions in regard to nearly all these points, but perhaps the most noticeable is the wide, flattened, and

divaricate form of their maxillary processes (see figs. 5 and 7). As regards this last point, and others, the Jack-Snipe is an aberrant Gallinagine form.

Attention is here directed to the totally different nature of the premaxilla of the Painted Snipe (*cf.* fig. 1). It is quite unlike that of any other form of Wader. It is neither Rusticoline nor Gallinagine nor Eroliine, but might be looked upon as aberrantly Tringine. I can see in it no Ralline similarity. In *Homoptilura* the premaxilla is more Gallinagine than Rusticoline.

Finally, there is another point, viz., one in connection with the slope of the outer processes of the nasals. In the Woodcock and Chatham Island Snipe these slope gently forwards, making a very obtuse angle with the horizon. In *Gallinago* and *Lymnocryptes* the slope is more violent and the angle made with the horizon much less obtuse. In the actual specimens this point is more striking than it might appear from a description, so that in this respect the four forms group themselves into a Rusticoline pair and a Gallinagine pair.

In *Rhynchæa* the outer nasal processes proceed forwards in the same plane with and also virtually parallel with the inner nasal processes—which is an anomalous condition, quite peculiar in itself. The angle made with the horizon is very obtuse indeed.

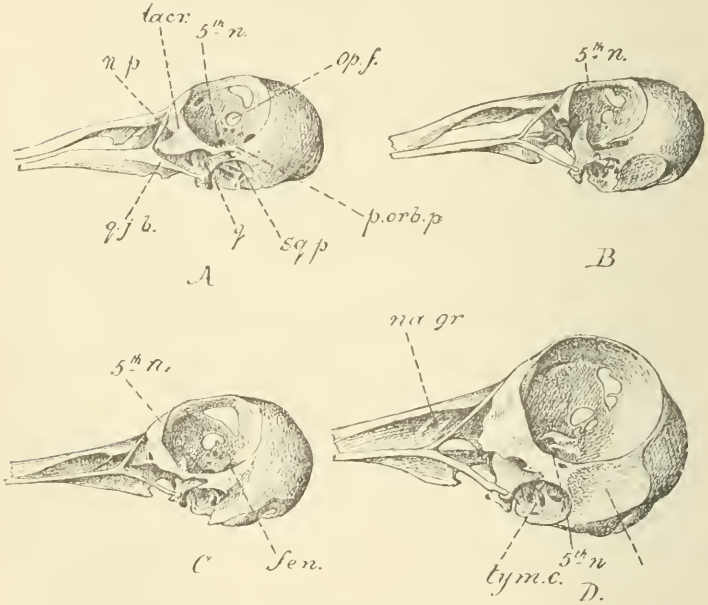
Skull viewed from the lateral aspect.

Viewed from this aspect the skull of the Chatham Island Snipe presents a feature which at once arrests our attention and marks this form as a particularly interesting one. In the Snipes of the genera *Scolopax*, *Gallinago*, and *Lymnocryptes*, an examination of the skulls reveals the fact that the descending process of the lacrymal, after almost losing its identity by fusion with the antorbital plate, is apparently continued as a thin ribbon-like plate of bone downwards and backwards, to eventually meet and fuse with the post-orbital process of the squamosal, so as to make the orbital rim as

complete in front and below as it is above and behind (*cf.* text-figures 12, A, C, D).

In the Chatham Island Snipe, on the other hand—and this is perhaps its most interesting feature,—the descending process of the lacrymal after fusing with the extero-anterior surface of the antorbital plate is abruptly arrested in its

Text-figure 12.



Lateral view of the skulls of:—A. *Lymnocryptes gallinula*; B. *Cœnocorypha pusilla*; C. *Gallinago gallinago*; D. *Scolopax rusticola*.

fen., fenestra; *lacr.*, lacrymal; *na.gr.*, nasal groove; *n.p.*, nasal process; *op.f.*, optic foramen; *q.j.b.*, quadratojugal bar; *q.*, quadrate; *p.orb.p.*, postorbital processes; *sq.p.*, squamosal process; *tymp.c.*, tympanic cavity; *5th n.*, foramen of 5th nerve.

course, and neither it nor the antorbital plate is continued downwards and backwards to join with the squamosal processes. *As a result, this antero-inferior portion of the orbital rim is deficient.*

We therefore get a very similar condition of things to that which obtains in the rest of the Waders, in

which we get no orbital rim below and in which we obtain an uninterrupted view of the whole of the quadrate (*cf.* text-figure 12, B).

This deficiency of the antero-inferior portion of the orbital rim, in a form which is undoubtedly Scolopacine, might very naturally be thought to be due to its having been lost in the specimen examined, or to its having broken away in the preparation of the skull, especially as there was only one skull available for examination. That this is not the case is rendered certain by the comparative examination carried out on seven or eight fossil examples of *C. chathamica*, and two of *C. pusilla*, in which exactly the same anatomical peculiarities are observable.

While the orbital rim in *C. pusilla* is deficient to this extent, it is to be noted, however, that the postorbital and squamosal processes, although preserving their identity, have been pushed or rotated forwards as if foreshadowing a complete union with the lacrymal or antorbital plate (*cf.* text-fig. 12, B). In this rotation forwards the quadrate, tympanic cavity, pterygoids, and palatines have shared. The amount of rotation forwards may be appreciated by noting the position of the quadrate in comparison with its position in a type like *Erolia*. Attention is also called to the large squamosal process in *C. pusilla*, and its gradual diminution in the Common and Jack-Snipe until its identity is practically lost in the Woodcock (*cf.* figures). In the Woodcock the postorbital and squamosal processes will be noticed to have been carried forwards to a greater extent than in the other three forms depicted in the text-figure.

The consideration of this rotation forwards of the inferior portions of the skull (in conjunction with the rotation backwards of other parts) brings us to a consideration of the *relative position of the quadrate* in the forms we have under consideration:—

(1) In the Woodcock the quadrate may be said to be extraorbital, since it has been pushed so far forward as to occupy a position below and in front of the orbital rim of bone forming the antero-inferior margin of the orbital

vacuity. Its ascending or orbital process lies parallel with and in the same plane as the descending lacrymal, by which it is very nearly completely hidden.

(2) In the Jack-Snipe the position of the quadrate is further back, and, shortly put, its ascending process may be said to lie neither inside nor outside the orbital space.

(3) In the Common Snipe the ascending process of the quadrate is intraorbital. It is seen projecting upwards caudad of the descending process of the lacrymal. The quadrate of the Common Snipe occupies, therefore, a position which is relatively further back than is the case with either the Woodcock or the Jack-Snipe.

(4) In the Chatham Island Snipe the quadrate lies further back still than it does in the Common Snipe.

(5) Finally, in the case of the Dunlin and its allies, as well as in *Rhynchæa*, the quadrate occupies a position which may be said to be normal for the Sandpipers, viz., one which is caudad of any of the above forms (*cf.* Pl. VIII. figs. 1 and 3).

On Plate VIII. the relative positions of the quadrate may be further studied from the dorsal aspect, and here we may observe that, as compared with the condition of things to be noted in the Dunlin and Painted Snipe, the more distad position of the quadrate and other neighbouring structures in the Chatham Island Snipe is well seen.

Associated with the forward position of the quadrate and other neighbouring structures, in the forms represented in text-figure 12, A, B, C, D, we may also call attention to the forward position of the foramina for the exit of the lower branches of the 5th nerve. The presence of fenestra in the alisphenoid, so well seen in figs. 5 and 6 on Pl. VIII., appears to be a Gallinagine character rather than a Rusticoline, although in some Woodcock skulls the presence of these is very faintly indicated. In one specimen examined it was indicated only on one side. The fenestra are potential

rather than actual, being covered with a transparent film. They are also indicated in *Homoptilura*. Other points to be noticed from a lateral view of the skulls under consideration are as follows :—

(1) The relative length of the quadrato-jugal bar, as compared with the outer process of the nasal of either side, and their relative shapes.

In the Rusticoline type these processes are as nearly as possible equal, and if an imaginary line be drawn, so as to join their proximal extremities, an equilateral triangle is produced. In the Rusticoline type both these processes are, moreover, flattened or ribbon-shaped, and their angle of junction is acute. In respect of both these characters the Chatham Island Snipe is Rusticoline, although these points in text-figure 12, B are not quite clearly shown. *Homoptilura* is also Rusticoline in this respect.

In the typical Gallinagine form the quadrato-jugal bar is distinctly longer than the outer nasal process, and makes a right angle with it. Both processes are thin and rounded, instead of flattened. In the Jack-Snipe much the same condition as regards relative length of these bones and the angle formed at their junction is to be noticed, but in this form there is a considerable amount of abnormality in the form and shape of the maxilla and jugal. In the Painted Snipe the condition observed is Tringine, in the Dunlin Eroliine (for differences, compare 'Ibis,' 1915, p. 615).

(2) In the Chatham Island Snipe and in the Jack-Snipe the internasal septum is markedly deficient, as compared with the conditions noticed in the Woodcock and Common Snipe (and its allies, so far as my investigations have extended).

In both these latter forms the groove for the nasal branch of the 5th nerve is a prominent feature (*cf.* text-figures 12, C and D). In the Chatham Island Snipe and the Jack-Snipe the lower end of the nasal groove is notched or deficient.

(3) In both the Chatham Island Snipe and the Jack-Snipe the high culmen-ridge is a noticeable character. In *C. pusilla* the slope formed by the nasal processes of the premaxillæ is identical with a line representing the inter-orbital slope, and this condition is also noted in the Dunlin. The flattened edge of the orbital margin is to be noted in *C. pusilla*.

(4) Another very striking feature common to both the Woodcock and the Chatham Island Snipe is the flat, somewhat quadrilateral, and slightly roughened plane immediately posterior to the tympanic cavity. This is most highly developed in the Woodcock, and, so far as I am aware, has not previously been remarked upon. For want of a better term I have called it the squamosal plane. It is well marked in *Homoptilura*.

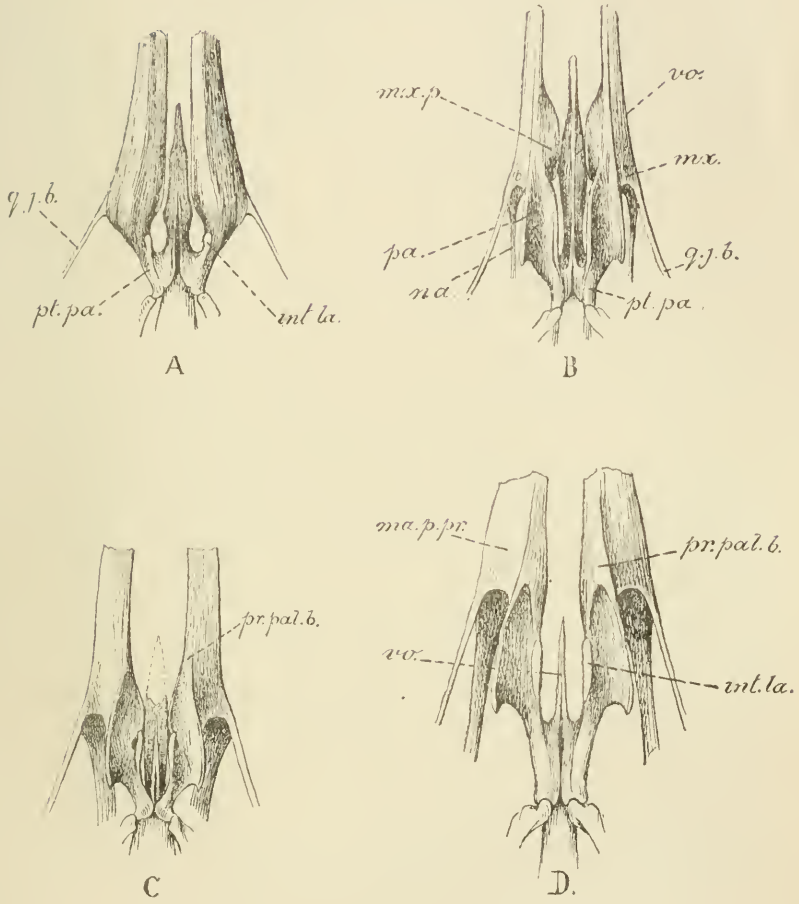
(5) Differences in the form and shape of the orbital rim are also to be noted:—In the Chatham Island Snipe this may be described as taking the form of an incompleted rhomboid with its angles rounded off—that is to say, it is reminiscent of the shape of the orbital rim in *Erolia*.

In the Woodcock the orbital rim is nearly circular, in the Common Snipe it is more nearly oval; while in the Jack-Snipe the rim is somewhat more circular than is the case with the Common Snipe.

The ventral aspect of the skull.

Transferring our attention from the lateral to the inferior aspect of the skull, we may direct attention more especially to the palatal region. In text-figure 13 the palatal region in the Chatham Island Snipe, Woodcock, Common Snipe, and Jack-Snipe is depicted, and the first thing which strikes one in a comparative examination of this region in the forms under consideration is the fact that, in as far as the several structures composing this region are concerned, the Chatham Island Snipe is neither Gallinagine nor quite typically Rusticoline. It may be said, however, to be much more

Text-figure 13.



Palatal region of:—A. *Lymnocryptes*; B. *Gallinago*; C. *Cœnocorypha*; D. *Scolopax*.

Int.la., inner lamina of the palatine; *mx.*, maxilla; *mx.p.*, maxillo-palatine process; *ma.p.pr.*, maxillary process of premaxilla; *na.*, outer nasal process of nasal bone; *pa.*, palatal plate; *pr.pal.b.*, prepalatal bar; *pt.pa.*, pterygoid process of palatine; *q.j.b.*, quadrato-jugal bar; *vo.*, vomer.

Rusticoline than Gallinagine. Leaving out of consideration for the present the palatal region of the Jack-Snipe, attention is directed to the following points as regards the palatal region of the other three forms :—

(*a*) In all three forms the postero-external angle of the palatal plate is prolonged backwards in a hook-shaped or falcate process, and this appears to be a special Scolopacine character (*cf.* Ibis, 1915, p. 612).

(*b*) In the Woodcock and Chatham Island Snipe the palatal plates are relatively shorter and wider than in the Common Snipe. The pterygoid processes of these structures in the two former types are, on the other hand, longer and more specialised at the expense of the palatal plate.

(*c*) In the Common Snipe the palatal portions of the maxillo-palatines are well developed, projecting inwards on either side to such an extent that they just fail to touch the outer margins of the vomer. They are long, narrow, and only slightly scroll-like structures, which have fused with the pre-palatal processes of the palatines throughout their whole extent.

In the Chatham Island Snipe the maxillo-palatines have also fused with the pre-palatal processes of the palatines, but their identity is not nearly so evident as in the Common Snipe. Their inner borders are slightly inverted or directed downwards, and they similarly just fail to touch the outer margin of the vomer of either side.

In the Woodcock the identity of the maxillo-palatines as viewed from this aspect is practically lost, and the free end of the vomer occupies an isolated position.

(*d*) In both the Chatham Island Snipe and the Woodcock the inner laminæ of the palatal plates are thickened and specialised, in contrast to those of the Common Snipe.

The forwardly projecting spur in which the inner laminæ of the palatal plate ends at its upper and anterior angle seems to be a Rusticoline character. It is present in *Scolopax* and *Cœnocorypha* (and was seen in fossil examples

of the latter) but is not present in *Gallinago*. In this latter the distal end of the lamina glides away into and merges with the pre-palatine bar, on which it is lost.

Attention is also called to the following points :—

(*e*) The different form and structural features of the vomer in all three types, and especially to its diminutive proportions in the Woodcock. The reader will also note the different structural details in the bifid posterior extremities of the three vomers.

(*f*) The relative position of the maxillary in all three forms, its fenestration in the Common Snipe, and the Rusticoline character of this bone in the Chatham Island Snipe.

(*g*) The much thicker, wider, and flatter nasals in the Woodcock and Chatham Island Snipe and the more massive maxillary processes of their premaxillæ.

As regards the palatal region of the Jack-Snipe, it will be noticed that this has been so highly specialised as to present features which seem to be absolutely unique. So far as I am aware, this region in the Jack-Snipe has never been previously described. In stating the case for the generic differentiation of this form under the name *Lymnocryptes*, previous authors have confined their attention to the double notching of the posterior margin of the sternum (a very unreliable character), to the distinctive features of the syrinx, or to the aberrant nature of the coloration and colour-pattern of the plumage. Apparently they have quite overlooked the highly interesting morphology of the palatal region, which ought to justify or settle for ever the claim of the Jack-Snipe to distinctive generic rank.

In a way of speaking, the only part of the palatines of the Jack-Snipe which are "visible" are their pterygoid processes and the internal laminæ (interpalatine laminæ), which appear to have been pushed considerably backwards and to terminate anteriorly in conspicuous, forwardly projecting, and rounded processes. All the rest of the palatal plates, maxillo-palatines, and pre-palatal bars of either side, together

with most of the maxillary and the maxillary process of the premaxilla, are involved or enwrapped in an elongate bony mass which forms a kind of pneumatic casing to these structures (*cf.* text-fig. 13, A). This peculiar pneumatic casing has the form of a very attenuated cone with its apex directed forwards. Distad it gradually merges with and is lost on the maxillary process of the premaxilla of either side (*cf.* text-fig. 13, A), proximad its base gradually merges with the pterygoid process of the palatal plate. It is to be noted that the outer nasal processes are not visible in this ventral view of the palatal region of *Lymnocryptes*, since they are hidden in the actual skeleton by a forwardly projecting plate of bone given off from the mesethmoid.

As regards other characters of the ventral aspect of the skull, it may be shortly stated that the form, structure, and disposition of the occipitals, basioccipital, precondylar fossa, foramen magnum, foramina for cranial nerves, basisphenoid, basitemporal, and pterygoids in *C. pusilla* are all Rusticoline, rather than Gallinagine. The lambdoidal ridge is not so well marked as in *Scolopax*.

A feature possessed by *Cœnocorypha*, and which is very characteristic of the Scolopacinæ, is the manner in which the basisphenoidal rostrum together with the basisphenoids and basitemporal are bent sharply upwards so as to make an obvious angle with the basioccipital. This Scolopacine character is rendered very obvious if the base of the skull of an Eroliine or a Tringine Wader is compared with that of a true Snipe. In the Jack-Snipe, however, the condition is not so marked. In *Rhynchæa* the condition is Tringine.

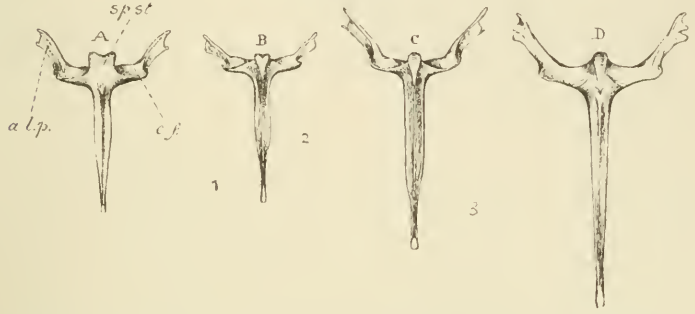
Other skeletal characters of Cœnocorypha.

As regards the rest of the skeletal structures of *C. pusilla*, I shall simply refer to a few points which seem worthy of notice :—

Sternum.—Although the arrangement of the notching at the hinder end of the sternal plate seems—at any rate, in regard to the Waders—to help us very little from a taxonomic standpoint, and, indeed, to be at times more misleading

than useful, yet it may be pointed out that in *C. pusilla* the notching of this part of the sternum is typically Gallinagine in character (that is to say, that it agrees exactly with the condition found in the Common Snipe). How unreliable this character is, may be gathered from the fact that the hinder margin of the sternum in the Painted Snipe presents the same Gallinagine* features, while, on the other hand,

Text-figure 14.



Anterior view of the sterna of:—A. *Cœnocorypha*; B. *Lymnocryptes*; C. *Gallinago*; D. *Scolopax*.

a.l.p., anterior lateral process; *c.f.*, coracoidal facet; *sp.st.*, spina sterni.

in regard to its skull, there is practically not a single Gallinagine character which I can discover. In the Jack-Snipe, too, this part of the sternum is four-notched, while in the Woodcock a fenestrated condition is to be noted in the region of the inner notch.

With regard to the forward end of the sternum, an examination of text-figure 14 reveals the fact that in *Scolopax*, *Gallinago*, *Lymnocryptes*, and *Cœnocorypha* the structural peculiarities of the coracoidal facets and the *spina sterni* have their own distinctive features.

In *C. pusilla* however the spina sterni is worth noting. It is bifid and wide from side to side, is seated directly between

* Taking the sum of the characters presented by the sternum of *Rhynchæa*, it would seem to be a nice point to decide whether they leant towards a Gallinagine, a Ralline, or a Jacanidine picture.

the coracoidal articulating facets, and looks directly upwards and slightly forwards. It is to be noted that the spina sterni of the Jack-Snipe has also a tendency to be bifid.

The coracoidal facets of the Woodcock are somewhat specialised. In all four forms the shape of the anterior lateral process is distinctively peculiar. This is especially evident in the Woodcock, but *C. pusilla*, in respect of the form of this process, agrees with the Woodcock rather than with the Snipe. The hypocleideum in *C. pusilla* is Gallinagine rather than Rusticoline. In the latter form it is very long and narrow. The carina of *C. pusilla* shows no evidence of degeneration.

Pelvis.—In *C. pusilla* it may be shortly said that the characters presented by the pelvis are, on the whole, more Gallinagine than Rusticoline. It is to be noted, however, that the upper margins of the preacetabular ilia are separated from one another and from the line of the vertebral spines by a considerable distance, and in this respect they present a Rusticoline character. It may also be pointed out that in *Scolopax rusticola* the iliac recesses for the lodgement of the kidneys present posteriorly the form of deep and conspicuous angular pouches, triangular in section and with flattened sides, converging to a sharp apex. The iliac ridges which mark the commencement of these pouch-like recesses are sharp, thin, and conspicuous. These sharply marked renal fossæ are apparently peculiar to the purely Rusticoline form, but there is a suggestion of them in *C. pusilla*, which is quite absent in the Common Snipe.

In *Rhynchæa* the pelvis presents features which, in respect of the blunt or square-ended preacetabular ilia and the somewhat pocket-like renal fossæ, are reminiscent of the Scolopacinæ ; the pectineal processes are conspicuous by their absence, however, and there is not the slightest hint of Ralline factors in the configuration of the whole pelvis.

As regards the arm and leg bones of *C. pusilla*, I do not propose to offer any remarks, beyond pointing out, that in the matter of length, the humerus, ulna, and middle metacarpus (+ phalanges) are all equal ; whereas in *Gallinago*

and *Lymnocryptes* the ulna is longer than the humerus, and the metacarpus (+phalanges) than the ulna. The ectepicondylar process in *C. pusilla* is ill developed.

Conclusions and Queries.

(1) *Cœnocorypha pusilla* is neither a typical Woodcock nor a typical Snipe, although it is much more Rusticoline than Gallinagine. It appears to be a generalised or primitive Scolopacine form. It may possibly be regarded as a relic of an ancient stock which at one time had a more northerly or a more general distribution, and from which stock the present-day Woodcocks and Snipes arose by still further specialisation.

(2) The status of the genus *Cœnocorypha*, originated by Gray and re-instated by Mr. G. M. Mathews (Ibis, 1913, p. 261), is amply confirmed by osteological examination. It is interesting to note that neither Gray, Seebohm, nor Mathews had studied the skeletal features of this form, but that, nevertheless, by the examination of what are generally held to be superficial characters, they arrived at a near appreciation of the peculiarities of this interesting Snipe-like form.

(3) Judging merely by the only form (*Homoptilura undulata gigantea*) whose skull I have been able to examine, the South American "semi-Woodcocks" have no close affinity with the "semi-Woodcocks" of the New Zealand subregion. It appears probable that they represent relics of ancient disconnected stages in the evolution of the true Woodcocks from a primitive Snipe-like form.

(4) The exact relationships of the Eroliinæ (the Dunlin association) to the Scolopacinæ would form an interesting subject of debate. Do the former represent a more direct and progressive line of descent from some common ancestral stock? Are the latter merely specialised and indirect offsets from this same stock? Does *Cœnocorypha* represent one of the first stages in the gradual process of evolution of the

true Snipe-form from the Eroliine stirp, or do the Woodcocks, the Snipes, the Jack-Snipe, and the Chatham Island Snipe merely represent so many sudden mutational forms derived from a common but independent Scolopacine stock?

(5) The so-called Painted Snipe (*Rhynchæa*) is neither Scolopacine nor Ralline. It is, however, Limicoline, possibly a surviving relic of a primitive Limicoline stock.

(6) Judging from the slight change in the relative proportions of the constituent bones of the pectoral limb and the absence of any signs of degeneration in the carina of the sternum, the diminishing powers of flight in *C. pusilla* is not a matter of long standing.

(7) *Coenocorypha pusilla* and its antipodean allies are "living fossils." They belong, strictly speaking, not to the present, but to a past geological period. The fact that they still exist and that we are still privileged to see them "in the flesh" is an 'accident,' the result of the isolation of the Chathams, Aucklands, and Snares, and their consequent freedom until recent times from carnivorous animals. They have persisted in this their last ultra-southern retreat beyond, so to speak, the allotted span of their race, and we may reasonably regard this generalised genus of "Snipes" as having formerly a much more extended distribution.

XXXVI.—*Note on the Nestling Plumage of the Asiatic Golden Plover* (Charadrius dominicanus fulvus). By Maud D. Haviland.

The young of this species was first described by Mr. H. L. Popham (Ibis, 1898, p. 512) from specimens that he obtained on the lower Yenesei. He describes it as being more spotted, with white about the sides of the head and neck, than are the young of *Charadrius apricarius*.

On July 20, 1914, I obtained four newly-hatched chicks from an identified nest on the tundra near Golchika, lower